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Thinning method and intensity influence long-term mortality trends in a red pine forest

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ABSTRACT

Tree mortality shapes forest development, but rising mortality can represent lost production or an adverse response to changing environmental conditions. Thinning represents a strategy for reducing mortality rates, but different thinning techniques and intensities could have varying impacts depending on how they alter stand structure. We analyzed trends in stand structure, relative density, stand-scale mortality, climate, and correlations between mortality and climate over 46 years of thinning treatments in a red pine forest in Northern Minnesota, USA to examine how thinning techniques that remove trees of different crown classes interact with growing stock manipulation to impact patterns of tree mortality. Relative density in unharvested plots increased during the first 25 years of the study to around 80%, then began to plateau, but was lower (12–62%) in thinned stands. Mortality in unharvested plots claimed 2.5 times more stems yr^{-1} and 8.6 times as large a proportion of annual biomass increment during the last 21 years of the study compared to the first 25 years, but showed few temporal trends in thinned stands. Mortality in thinning treatments was generally lower than in controls, particularly during the last 21 years of the study when mortality averaged about 0.1% of stems yr^{-1} and 4% of biomass increment across thinning treatments, but 0.8% of stems yr^{-1} and 49% of biomass increment in unharvested plots. Treatments that combined thinning from above with low growing stock levels represented an exception, where mortality exceeded biomass production after initial thinning. Mortality averaged less than 0.1% of stems yr^{-1} and less than 1% of annual biomass production in stands thinned from below. These trends suggest thinning from below minimizes mortality across a wide range of growing stock levels while thinning from above to low growing stock levels can result in dramatic short-term increases in mortality. Moderate to high growing stock levels (21–34 m^2 ha^{-1}) may offer greater flexibility for limiting mortality across a range of thinning methods. Mean and maximum annual and growing season temperatures rose by 0.6–1.8 °C during the study, and temperature variables were positively correlated with mortality in unharvested plots. Mortality increases in unharvested plots, however, were consistent with self-thinning principles and probably not driven by rising temperatures. These results suggest interactions between thinning method and intensity influence mortality reductions associated with thinning, and demonstrate the need for broader consideration of developmental processes as potential explanations for increased tree mortality rates in recent decades.

1. Introduction

Mortality is an integral process in forest development that can inform us about competitive interactions that shape a stand's developmental trajectory, help predict productivity, and alert us to responses to environmental change that fall outside the system's natural or historical range of variability (Franklin et al., 1987; Allen et al., 2010). As changes in societal demands for goods and services from forests drive changes in forest management, there is an increasing need to understand how different management practices influence key ecological processes like tree mortality. A plant's demand for resources increases as it grows, leading to predictable relationships between mean plant size and the number of individuals that can be supported in a given area (Reineke, 1933; Yoda et al., 1963). This relationship is generally expressed through a power function that specifies the maximum size–density boundary line for a given species. In forests, density-dependent mortality is often described using the concept of relative density, the ratio of

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observed stand density to the maximum density that could occur in a stand of the same mean tree size or volume (Drew and Flewelling, 1979). Density-dependent mortality, or self-thinning, can occur when stand conditions enter a "zone of imminent competition-mortality" (Drew and Flewelling, 1977), which is bounded by a minimum relative density necessary for competition-induced mortality and the maximum size–density boundary line for a given species. Silvicultural practices that reduce stand densities (thinning) can minimize mortality by maintaining relative densities below the zone of imminent competition-mortality.

While size–density relationships describe expected patterns of stand-scale mortality, a variety of other mechanisms may influence mortality in individual trees. Individual tree mortality often displays a U-shaped relationship with tree size such that small trees and very large trees are more likely to die than intermediate-sized trees (Lorimer et al., 2001; Busing, 2005; Fraver et al., 2008). While an increased probability of mortality for small trees is common across most forests, the high mortality rates observed for very large trees may only apply to old-growth forests where the largest trees may represent a senescent overstory component with increased vulnerability to windthrow, disease, and other mortality agents (Goff and West, 1975; Lorimer et al., 2001). Tree vigor may also influence mortality responses to stand density reductions. Although growth-mortality relationships are highly variable among species (Wyckoff and Clark, 2002; Wunder et al., 2008), slow-growing trees of a given species generally have higher probabilities of death than their faster growing neighbors (Bigler et al., 2004, 2007; Fraver et al., 2008). This suggests thinning treatments that remove primarily smaller, less vigorous trees in understory or suppressed canopy positions are likely to be more effective at reducing mortality than treatments that remove larger, faster growing trees in dominant or codominant canopy positions.

Thinning to different residual densities or stocking levels is also likely to produce varying effects on tree mortality. If resource availability and competition were the only influences on tree death, then density-dependent mortality should lead to a higher probability of tree death in denser neighborhood environments (Kenkel, 1988; He and Duncan, 2000). In reality, however, trees with different characteristics may show contrasting responses to the same neighborhood environment. For example, small trees growing in less crowded environments have a lower probability of mortality because of reduced competition (Uriarte et al., 2004), while large trees in similar environments have a higher probability of windthrow because of increased crown exposure (Canham et al., 2001; Thorpe et al., 2008).

Recent studies also suggest that rising temperatures and corresponding changes in hydrology and water deficits lead to greater drought stress and increased tree mortality (Guarín and Taylor, 2005; Bigler et al., 2007; van Mantgem and Stephenson, 2007; Millar et al., 2007; Breshears et al., 2009; van Mantgem et al., 2009; Allen et al., 2010). Reducing stand densities through thinning treatments has been suggested as a mechanism to increase a forests' resilience to rising temperatures and drought stress (McDowell et al., 2006; Battles et al., 2008; Voelker et al., 2008). While thinning may reduce drought stress in some forests, it is not clear that thinning would effectively increase resilience in different forest types or regions, and specific recommendations for target densities or growing stock levels to reduce mortality during periods of warming are lacking.

The complicated interactions following harvesting and the potential differences between short- and long-term responses to treatments make it difficult to understand the utility of thinning in reducing mortality. Results from controlled, replicated studies with multi-decadal datasets are needed to assess the effects of various thinning treatments on mortality. A long-term study of red pine (*Pinus resinosa* Ait.) stands in Northern Minnesota, USA, provided an excellent opportunity to assess the influence of thinning on mortality risk. We examined tree mortality over a 46-year period in stands treated with various thinning methods that both preferentially removed different-sized trees and maintained growing stock levels (i.e. thinning intensities) across a range of basal areas. Our objectives were to (1) examine changes in stand structure and relative density that could contribute to differences in mortality among different thinning methods and growing stock levels; (2) determine how interactions between thinning method and intensity influence stand-scale mortality; and (3) assess the extent to which changes in temperature, precipitation, and drought severity during the study period may have contributed to tree mortality.

2. Materials and methods

2.1. Study sites and inventory measurements

We used data from the Birch Lake Thinning Study, a long-term silvicultural experiment in red pine stands, planted in 1912, on the Superior National Forest in northeastern Minnesota, USA. The area has a continental climate, with an average annual temperature of 4.1 °C, a maximum mean monthly temperature of 19.2 °C in July and a minimum mean monthly temperature of −14.1 °C in January. Annual precipitation averages 700.2 mm, with 88% of this total falling between the months of April and November. Soils are coarse-textured, excessively drained typic Udipsamments in the Entisol order. The site index for red pine was approximately 18 m at base age 50 years.

Eighteen 0.8 ha plots were randomly assigned either a thinning treatment to one of five residual growing stock levels (7, 14, 21, 28, and 34 m^2 ha^{-1}) or left as an untreated control. Three thinning methods (thin-from-above, thin-from-below, or combination) were nested within each plot for a total of three replicates of each thinning method *x* growing stock level treatment. Nested plots for thinning method treatments were approximately 0.27 ha. The thin-from-above treatment removed trees in dominant and codominant canopy positions, the thin-from-below treatment removed suppressed and intermediate trees, and the combination treatment removed trees more or less equally throughout the canopy profile. Plots were first thinned at age 45 in 1957, with repeated thinnings in 1962, 1972, 1982, 1992, and 2003 for the 21, 28, and 34 m^2 ha^{-1} treatments. The 7 and 14 m^2 ha^{-1} treatments were thinned only in 1957 and 1962. Red pine represented 99% of the basal area.

Tree measurements were made in 1957, 1962, 1967, 1972, 1976, 1982, 1987, 1992, and 2003 in three 0.08 ha subplots in each larger treatment plot (one subplot per thinning method per plot). Trees were tagged and stem-mapped so the status of each individual could be followed through time. Measurements were made prior to harvesting during treatment years, and included diameter at breast height (DBH, 1.37 m) of all trees >10 cm DBH, the height of two or three trees for each crown class in each plot, and the status (cut or dead) of any tree that had died or been cut since the previous inventory.

2.2. Data analysis

To address objective 1, we analyzed changes in stem density, quadratic mean diameter (QMD), and relative density using linear mixed models. Relative density was calculated using Reineke's stand density index (SDI, Reineke, 1933) where

$$\mathrm{SDI} = \text{Stem density} \times \left(\frac{25}{\mathrm{QMD}}\right)^{-1.605} \qquad (1)$$

Table 1
Results from linear mixed models testing the influence of growing stock level, thinning method, and measurement year on structural characteristics in a red pine forest in Northern Minnesota, USA.

Independent variable[a]	Log (stem density)			Quadratic mean diameter			Relative density		
	DF	*F* value	*P*-value	DF	*F* value	*P*-value	DF	*F* value	*P*-value
GSL	4	24.09	<0.001	4	3.01	0.019	4	114.02	<0.001
TM	2	17.58	<0.001	2	14.73	<0.001	2	11.11	0.001
GSL × TM	8	1.00	0.439	8	1.04	0.405	8	1.10	0.364
YR	8	939.21	<0.001	8	759.54	<0.001	8	620.32	<0.001
GSL × YR	32	145.42	<0.001	32	16.10	<0.001	32	132.87	<0.001
TM × YR	16	13.67	<0.001	16	32.84	<0.001	16	1.61	0.066
GSL × TM × YR	64	2.93	<0.001	64	5.75	<0.001	64	1.23	0.128
R^2		0.991			0.988			0.993	
RMSE		0.142			1.929			2.916	

[a] GSL: growing stock level; TM: thinning method; YR: measurement year.

After calculating SDI values for each plot and measurement year, relative density was calculated as:

$$\text{Relative density}\,(\%) = 100 \times \frac{\text{SDI}_{\text{obs}}}{\text{SDI}_{\text{max}}} \tag{2}$$

where SDI_{max} is the maximum possible (upper boundary) SDI value for a given stem density and SDI_{obs} is the calculated SDI for a given measurement year. SDI_{max} was calculated using an upper boundary line developed for density management diagrams for red pine in the Lake States region by Mack and Burk (2005). We included thinning method, growing stock level, and year of measurement as fixed-effects, a random effect to account for the nesting of thinning method plots within stands treated with different growing stock levels, and an autoregressive, heterogeneous covariance structure to account for repeated measurements on the same plots over time. Differences between treatment means were evaluated using Bonferroni-adjusted *t*-tests when our models indicated significant treatment effects. Trees that reached 10 cm DBH during a measurement interval (ingrowth) were included in calculations of structural characteristics (e.g., stem density, QMD, basal area) for all future measurement years. Ingrowth was primarily red pine.

To address our second objective, we calculated stand-scale mortality as a function of both stem density (MORT_{DEN}, $100 \times (d_i/(n_0 - c_i)/L_i)$) and aboveground biomass increment (MORT_{BMI}, $100 \times db_i/bm_i$) for each measurement period where d_i is the number of individuals that died during the period, n_0 is the number of individuals alive at the beginning of the period, c_i is the number of trees that were cut during the period, L_i is the period length (in years), db_i is the mean annual dead biomass production during the period, and bm_i is the mean annual live biomass increment for the period. Aboveground biomass was calculated for each sampling period using regionally-derived, species-specific allometric equations (Perala and Alban, 1994). Trees that reached 10 cm DBH during a measurement interval were included in mortality analyses for all subsequent years.

We used linear mixed models to analyze stand-scale mortality with either MORT_{DEN} or MORT_{BMI} as the dependent variable. We included thinning method, growing stock level, and measurement period (the interval between two measurement years) as fixed-effects, a random effect to account for the nesting of thinning method plots within stands treated with different growing stock levels, and an autoregressive, heterogeneous covariance structure to account for repeated measurements on the same plots over time. Efforts to analyze mortality trends using generalized linear mixed models (GLMMs) with poisson, negative binomial, zero-inflated poisson, and zero-inflated negative binomial distributions were hampered by convergence problems which could only be overcome by removing random effects from the model. Since temporal and spatial autocorrelation were likely in our spatially nested design with repeated measurements taken on the same plots over time, we felt it was important to develop models that account for these random effects rather than using a GLMM model without terms to account for the random effects. Analysis of residuals did not suggest extreme departures from normality in our linear mixed models. Differences between treatment means were evaluated using Bonferroni-adjusted *t*-tests when our models indicated significant treatment effects.

To address our third objective we analyzed climate over the study period using linear regression models with autoregressive error terms. We modeled changes in both annual and growing season maximum temperature, minimum temperature, mean temperature, precipitation, and the Palmer Drought Severity Index (PDSI) as functions of time for the entire study period (1957–2003). Annual precipitation and PDSI values were calculated by averaging monthly values for current water years (October through September). All annual climate data were calculated by averaging monthly values from a weather station in Ely, Minnesota located approximately 15 km north of the study area (NOAA, 2009). We tested for temporal autocorrelation using the Durbin–Watson statistic for first-order autocorrelation and generalized Durbin–Watson statistics for higher-order autocorrelation. The Portmanteau *Q* test was used to test for heteroscedasticity.

We calculated Pearson correlation coefficients between mortality and climate variables to assess relationships between patterns of tree death and fluctuations in temperature or precipitation during the study period. We used average mortality and the average for a given climate variable within each measurement interval as the experimental units for this analysis. Separate tests were conducted for each thinning treatment. Initial tests using lagged climate variables generally produced weaker relationships between mortality and climate than direct correlations between mortality and climate during the same years. All statistical tests were performed at the $\alpha = 0.05$ significance level using SAS version 9.2 (SAS Institute, Cary, NC).

3. Results

3.1. Stand structure

Stem density was influenced by growing stock level, thinning method, and measurement year, but temporal trends in stem density varied among growing stock levels and thinning methods (Table 1). Stem density decreased after the initial thinning in every thinning treatment, then remained relatively constant in the 7 $m^2\,ha^{-1}$ thin-from-above treatment and all 14 $m^2\,ha^{-1}$ treatments, but continued to decrease over time in all 21, 28, and 34 $m^2\,ha^{-1}$ thinning treatments (Fig. 1). Stem density declined slightly over time in unharvested control stands, but the rate of decline was much slower than in thinned stands where harvesting artificially reduced densities, such that stem densities were signif-

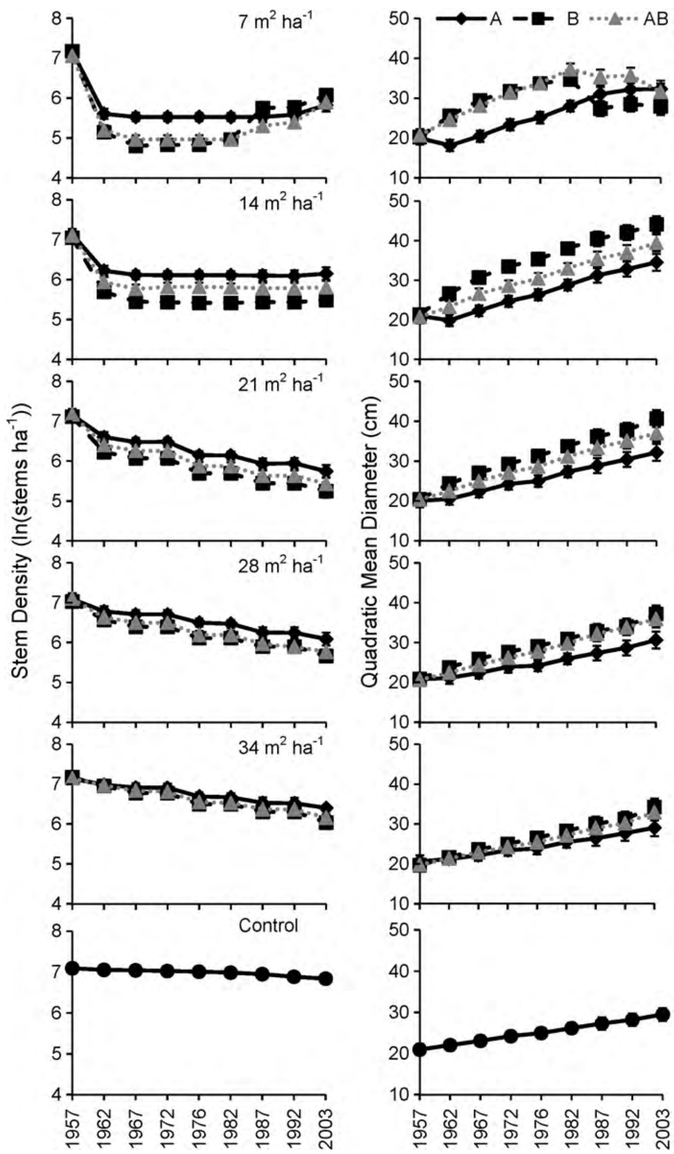

Fig. 1. Changes in stand structure during a long-term thinning experiment in a red pine forest in Northern Minnesota, USA. Error bars represent standard error, A = thin-from-above, B = thin-from-below, and AB = thin throughout the canopy profile. Thinning treatments were implemented after the 1957 measurement.

icantly higher in controls than in any thinned stands from 1967 onward. After the initial thinning, stem densities were generally greater in the 7, 14, 21, and 28 $m^2\ ha^{-1}$ thin-from-above treatments than in the same growing stock levels when thinned from below. There were no significant differences in stem densities among thinning methods in the 34 $m^2\ ha^{-1}$ treatment.

QMD was influenced by growing stock level, cutting method, measurement year, and temporal trends varied by growing stock level and cutting method, as well as among cutting methods within individual growing stock treatments (Table 1). QMD consistently increased over time in the 14, 21, 28, and 34 $m^2\ ha^{-1}$ treatments and unharvested control stands, regardless of thinning method (Fig. 1). QMD was higher in the 14, 21, and 28 $m^2\ ha^{-1}$ thin-from-below treatments than in the corresponding growing stock levels when thinned from above for all measurements from 1982 onward, but there were no differences among thinning methods in the 34 $m^2\ ha^{-1}$ treatment. There were no differences in QMD among stands prior to the initial thinning. QMD was generally lower in control stands than in stands that were thinned from below or thinned

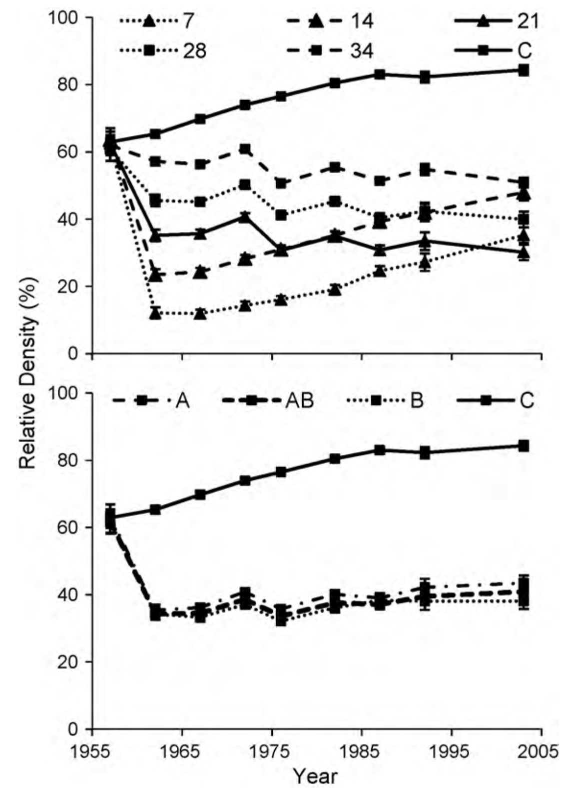

Fig. 2. Changes in relative density during a long-term thinning experiment in a red pine forest in Northern Minnesota, USA. Error bars represent standard error, numbered labels represent residual growing stock levels (in $m^2\ ha^{-1}$), A = thin-from-above, B = thin-from-below, AB = thin throughout the canopy profile, and C = unharvested control. Thinning treatments were implemented after the 1957 measurement.

using the combination method from 1982 onward, but there were no significant differences in QMD between control stands and stands thinned to 34 $m^2\ ha^{-1}$ or stands that were thinned from above during any measurement interval.

Relative density varied across cutting methods, growing stock levels, years, and the growing stock treatment effect varied over time (Table 1). There were no differences in relative density among plots prior to treatment, but relative density was significantly higher in the controls than in thinning treatments for all years after initial thinning (Fig. 2). Relative density increased steadily between measurement years in the controls until 1987, but there were no significant differences in relative density in control plots from 1987 to 2003. Relative density was ranked 34 $m^2\ ha^{-1}$ > 28 $m^2\ ha^{-1}$ > 21 $m^2\ ha^{-1}$ > 14 $m^2\ ha^{-1}$ > 7 $m^2\ ha^{-1}$ from 1962 to 1972, and 34 $m^2\ ha^{-1}$ > 28 $m^2\ ha^{-1}$ > 21 $m^2\ ha^{-1}$ in all later measurement years, but relative densities were higher in the 14 $m^2\ ha^{-1}$ treatment than the 21 and 28 $m^2\ ha^{-1}$ treatments by 2003, while relative density in the 7 $m^2\ ha^{-1}$ treatment was not significantly different from the 21 and 28 $m^2\ ha^{-1}$ treatment by 2003. Relative density in the 21, 28, and 34 $m^2\ ha^{-1}$ treatments varied among years, but generally decreased slightly from 1962 to 2003, while relative density in the 7 and 14 $m^2\ ha^{-1}$ treatments rose from 1967 to 2003 after thinning was stopped in these two treatments. Relative density was similar among the three cutting methods, but was higher in controls than in thinned stands regardless of cutting method (Fig. 2).

3.2. Stand-scale mortality as a function of tree density

Growing stock level, thinning method, measurement period, and all their interactions had significant effects on mortality

Table 2
Results from linear mixed models testing the influence of growing stock level, thinning method, and measurement year on stand-scale mortality in a red pine forest in Northern Minnesota, USA.

Independent variable[a]	Mortality as a function of density			Mortality as a function of biomass increment		
	DF	*F* value	*P*-value	DF	*F* value	*P*-value
GSL	4	3.53	0.008	4	0.40	0.806
TM	2	6.30	0.008	2	0.82	0.454
GSL × TM	8	2.85	0.005	8	0.90	0.515
YR	7	3.56	0.001	7	4.92	<0.001
GSL × YR	28	2.46	<0.001	28	1.44	0.074
TM × YR	14	2.98	<0.001	14	1.04	0.413
GSL × TM × YR	56	2.60	<0.001	56	1.84	0.001
R^2		0.821, 0.239			0.959, 0.509	
RMSE		0.469			36.530	

[a] GSL: growing stock level; TM: thinning method, YR: measurement year, R^2 values are for models with fixed + random effects, and fixed-effects only, respectively.

expressed as a function of density (Table 2). With the exception of the 7 and 14 $m^2\,ha^{-1}$ thin-from-above treatments, $MORT_{DEN}$ in the controls was generally similar to the thinned stands from 1957 to 1967, but mortality was higher in the controls than in most thinning treatments during many of the following measurement periods (Fig. 3). In comparing thinning methods, mortality was higher in the 7 $m^2\,ha^{-1}$ thin-from-above treatment than the 7 $m^2\,ha^{-1}$ thin-from-below or combination treatments from 1957 to 1967 and occasionally higher in other thin-from-above treatments than thin-from-below treatments or combination treatments at a given growing stock level in following years. $MORT_{DEN}$ was also occasionally higher in the combination thinning method than the thin-from-above or thin-from-below treatments at a given growing stock level, but mortality in the thin-from-below treatments was never significantly higher than mortality in the thin-from-above or combination treatments at any growing stock level.

When growing stock levels were compared, $MORT_{DEN}$ was higher in the 7 $m^2\,ha^{-1}$ thin-from-above treatment than any other thin-from-above treatment from 1957 to 1967, but there were few other differences among growing stock levels in the thin-from-above treatment in later measurement periods and no differences among growing stock levels in the thin-from-below treatment during any measurement period. $MORT_{DEN}$ was also generally similar among growing stock levels in the combination treatment. $MORT_{DEN}$ in the unthinned control treatment was higher in all measurement periods from 1976 to 2003 than in any period from 1967 to 1976, and generally rose over time. The only significant temporal trends within thinned stands were associated with high initial mortality in the 7 and 14 $m^2\,ha^{-1}$ thin-from-above treatments followed by lower mortality from 1967 onward.

3.3. *Stand-scale mortality as a function of biomass increment*

Only measurement period and the growing stock level by thinning method by measurement period interaction were significant when mortality was expressed as a function of aboveground biomass increment (Table 2). When thinning methods were compared, there were few differences in $MORT_{BMI}$ between controls and thinned stands from 1957 to 1972, but mortality was higher in controls than in most thinning treatments from 1972 to 1987 and from 1992 to 2003 (Fig. 4). $MORT_{BMI}$ was dramatically higher in the 7 $m^2\,ha^{-1}$ thin-from-above treatment than in the 7 $m^2\,ha^{-1}$ thin-from-below or combination treatments from 1957 to 1962, but no other thin-from-above treatment was ever significantly higher than the thin-from-below or combination treatments at the same growing stock level. $MORT_{BMI}$ was sometimes higher in the combination thinning method than in the thin-from-above or thin-from-below treatments at a given growing stock level. Mortality in the thin-from-below treatment was never significantly higher than mortality in the thin-from-above or combination treatments at any growing stock level.

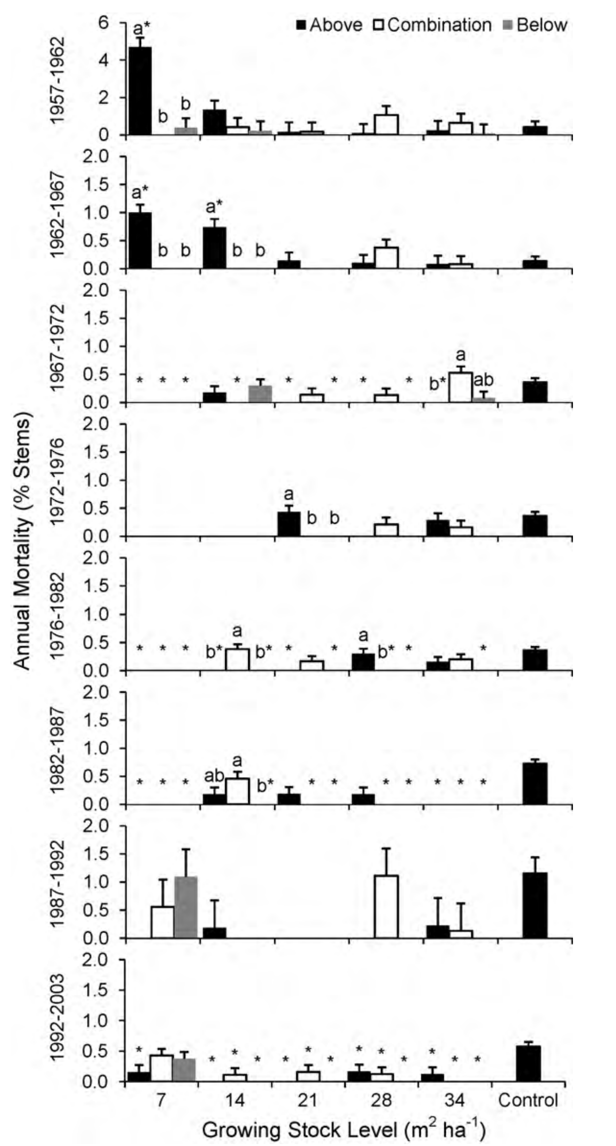

Fig. 3. Annual mortality expressed as a percentage of stem density in a long-term study of the effects of different thinning methods and growing stock levels in a red pine forest in Northern Minnesota, USA. Letters indicate significant differences among thinning methods within a given growing stock level, an asterisk indicates a significant difference from the control in a given measurement period, and error bars represent standard error. Note the different scale in the first row of panels.

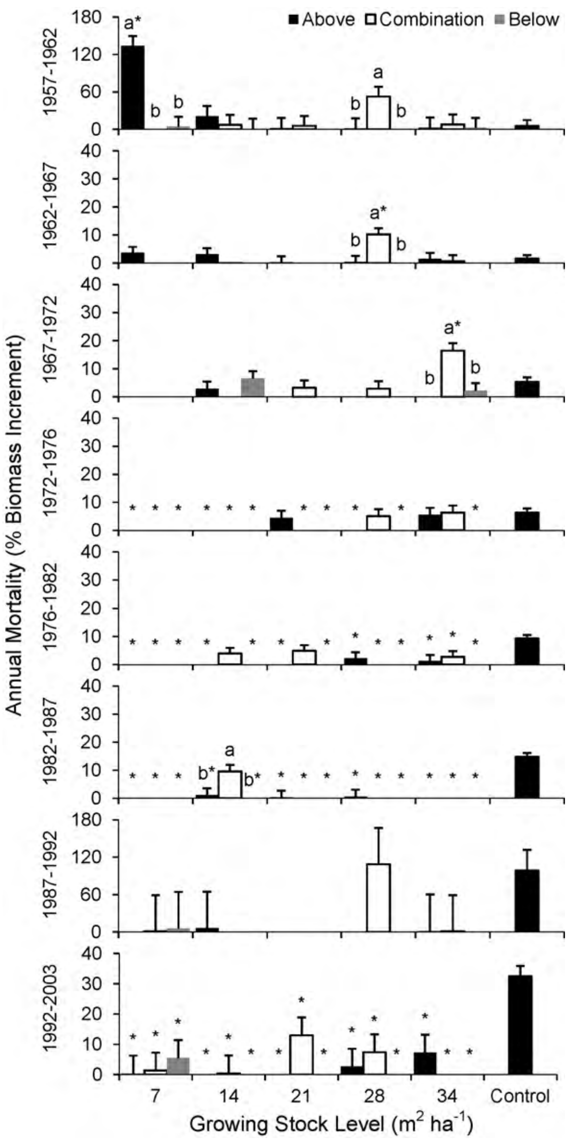

Fig. 4. Annual mortality expressed as a percentage of aboveground biomass increment in a long-term study of the effects of different thinning methods and growing stock levels in a red pine forest in Northern Minnesota, USA. Letters indicate significant differences among thinning methods within a given growing stock level, an asterisk indicates a significant difference from the control in a given measurement period, and error bars represent standard error. Note that the scale changes among rows of panels.

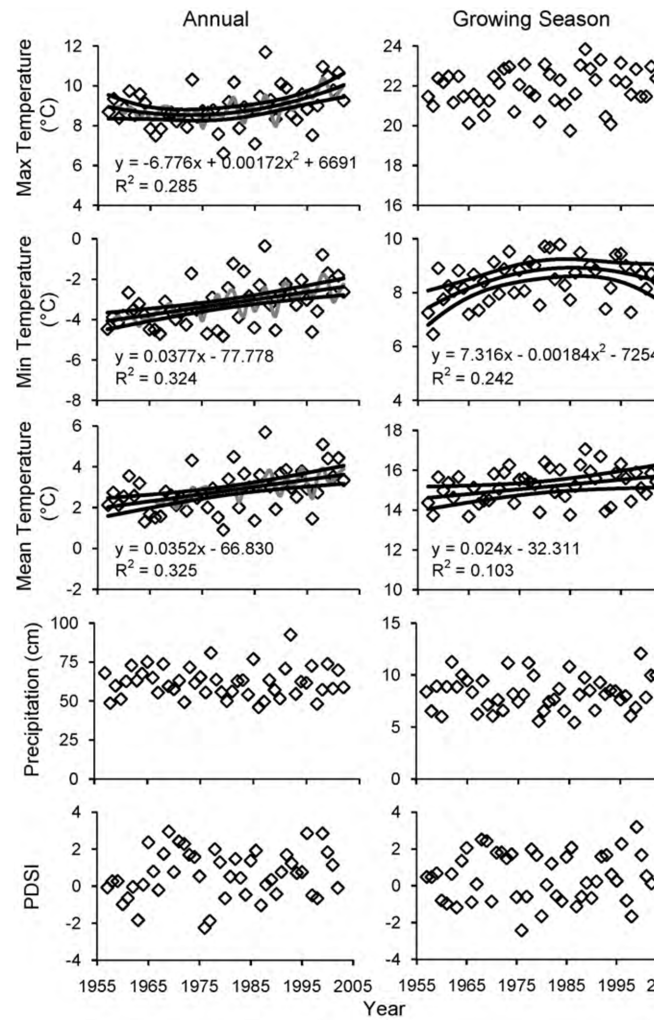

Fig. 5. Climate parameters over a 46-year period at a thinning experiment in Northern Minnesota, USA. Solid black lines indicate predicted relationships between a given parameter and time (when significant), dotted lines indicate 95% confidence limits, and gray lines indicate relationships with significant temporal autocorrelation. PDSI is the Palmer Drought Severity Index.

Among growing stock levels, $MORT_{BMI}$ was much higher in the 7 $m^2\ ha^{-1}$ thin-from-above treatment than in any other thin-from-above treatment from 1957 to 1962, but there were no significant differences among growing stock levels in the thin-from-above treatments in following years. $MORT_{BMI}$ sometimes varied among growing stock levels in the combination treatment, but was not consistently higher in any given growing stock level. There were no significant differences in mortality among growing stock levels in the thin-from-below treatments during the study. In the controls, $MORT_{BMI}$ was greater from 1987 to 2003 than during any preceding measurement period, greater from 1982 to 1987 than during any previous period except for 1957–1962, and greater from 1976 to 1982 than during the 1962–1967 measurement period. The only significant temporal trend in thin-from-above treatments was higher mortality from 1957 to 1962 at the 7 $m^2\ ha^{-1}$ growing stock level than in any following measurement period. $MORT_{BMI}$ was highly variable among years in the combination treatment at any given growing stock level, but there were no temporal trends in mortality in the thin-from-below treatments at any growing stock level.

3.4. Temporal trends in climate variables

Daily maximum and mean annual temperate generally increased during the course of the study, while precipitation and PDSI showed no significant changes during the 46-year study period whether expressed as current water year means or as growing season means (Fig. 5). Average maximum and mean annual temperature rose by 1.6° and 0.7°, respectively. There were no significant trends in average minimum annual temperature, annual precipitation, or annual PDSI. Average maximum and mean growing season temperature rose by 1.8° and 0.6°, respectively. Average minimum growing season temperature rose by about 1.0 during the first 22 years of the study period, but dropped by 1.6° during the next 24 years. There were no significant trends in growing season precipitation or PDSI.

3.5. Correlations between mortality and climate variables

Both $MORT_{DEN}$ and $MORT_{BMI}$ were correlated with several climate variables in unharvested control stands, but there were few

Table 3
Pearson correlation coefficients and *P*-values for correlations between mortality and climate variables in red pine stands thinned using various thinning methods and residual growing stock levels.

	Control		Above		Combination		Below		7 m² ha⁻¹		14 m² ha⁻¹		21 m² ha⁻¹		28 m² ha⁻¹		34 m² ha⁻¹	
	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value	PCC	*P*-value
Mortality as a function of density																		
Annual precipitation	0.501	0.206	−0.565	0.145	−0.286	0.492	0.032	0.940	−0.458	0.254	−0.549	0.158	0.017	0.969	−0.398	0.329	−0.332	0.422
Annual T_{max}	0.855	0.007	0.086	0.840	0.628	0.095	0.738	0.036	0.419	0.302	0.019	0.965	−0.384	0.348	0.620	0.101	−0.072	0.866
Annual T_{min}	0.425	0.294	0.079	0.853	0.251	0.549	0.126	0.766	0.067	0.874	0.135	0.749	0.256	0.540	0.194	0.645	0.260	0.533
Annual T_{mean}	0.871	0.005	0.106	0.802	0.607	0.110	0.625	0.098	0.352	0.392	−.085	0.841	−0.156	0.713	0.571	0.139	0.083	0.846
GS precipitation	0.860	0.006	−0.252	0.547	0.180	0.670	0.423	0.296	0.006	0.988	−0.363	0.377	−0.192	0.648	0.269	0.520	−0.380	0.354
GST_{max}	0.865	0.006	0.065	0.879	0.662	0.073	0.741	0.035	−.392	0.337	−.029	0.947	−0.423	0.297	0.634	0.091	−0.008	0.984
GST_{min}	0.321	0.438	−0.166	0.695	0.058	0.891	0.013	0.977	−0.181	0.669	−0.135	0.749	0.012	0.978	0.148	0.727	0.081	0.849
GST_{mean}	0.811	0.015	−0.045	0.916	0.517	0.190	0.549	0.159	0.186	0.659	−0.054	0.899	−0.303	0.466	0.546	0.162	0.039	0.927
Mortality as a function of biomass increment																		
Annual precipitation	0.276	0.508	−0.424	0.295	−0.068	0.873	0.063	0.882	−0.422	0.298	−0.294	0.480	−0.011	0.980	−0.081	0.849	0.083	0.845
Annual T_{max}	0.810	0.015	0.211	0.617	0.737	0.037	0.351	0.393	0.245	0.558	0.194	0.645	0.230	0.584	0.735	0.038	−0.347	0.400
Annual T_{min}	0.152	0.719	0.191	0.651	0.278	0.505	−0.115	0.786	0.187	0.658	0.370	0.367	−0.343	0.406	0.255	0.543	−0.037	0.931
Annual T_{mean}	0.693	0.057	0.260	0.535	0.704	0.051	0.205	0.626	0.284	0.495	0.342	0.407	−0.007	0.988	0.490	0.058	−0.282	0.499
GS precipitation	0.758	0.029	−0.153	0.718	0.457	0.255	−0.026	0.951	−0.137	0.745	−0.169	0.689	−0.006	0.988	0.516	0.191	−0.447	0.266
GST_{max}	0.815	0.014	0.202	0.631	0.761	0.028	0.335	0.417	0.239	0.569	0.224	0.593	0.162	0.702	.7529 × 4	0.031	−0.347	0.400
GST_{min}	0.245	0.559	−0.131	0.757	0.215	0.609	−0.379	0.354	−0.138	0.744	0.000	1.000	−0.587	0.126	0.270	0.518	−0.261	0.532
GST_{mean}	0.732	0.039	0.075	0.860	0.676	0.066	0.035	0.935	0.098	0.818	0.164	0.698	−0.207	0.622	0.701	0.053	−0.399	0.328

significant relationships between mortality and climate variables in thinned stands (Table 3). $MORT_{DEN}$ was positively correlated with annual maximum temperatures, annual mean temperatures, growing season average maximum temperatures, growing season mean temperatures, and growing season precipitation in control stands. The only significant relationships between $MORT_{DEN}$ and climate variables in thinned stands were positive correlations with annual and growing season mean daily maximum temperatures in stands that were thinned from below. $MORT_{BMI}$ was positively correlated with annual maximum temperatures, growing season maximum temperatures, growing season mean temperatures, and growing season precipitation in control stands. $MORT_{BMI}$ was also positively correlated with annual and growing season mean temperatures in stands that were thinned using the combination method, and in the 28 m^2 ha^{-1} growing stock treatment.

4. Discussion

Our results demonstrate a clear increase in stand-level mortality over a multi-decadal period of changing stand structural conditions in dense, unmanaged pine stands while stands that received thinning treatments generally did not show parallel increases in mortality. High initial mortality in some thinning treatments coupled with complex relationships between residual growing stock level, thinning method, and time, however, suggest care must be taken when prescribing silvicultural treatments designed to reduce mortality risk and increase resilience. Our findings suggest that the stand structures created by different thinning methods influence mortality and shed light on the interactions between thinning method, residual growing stock level, and time that were ultimately found for stand-level mortality (below).

Maximum size–density relationships likely explain the rising mortality rates in our control stands during this study. There is a well-established link between stand density, mean tree size, and competition-induced mortality in forests (Reineke, 1933; Drew and Flewelling, 1979; Jack and Long, 1996; Bravo-Oviedo et al., 2006). This link suggests that stands of a given mean tree size will support only a fixed stem density regulated by competition-induced mortality as stand density approaches this upper limit. Increasing QMD in our controls coupled with relatively small changes in stand densities led to rising SDI and relative density during the course of the study. Long (1985) suggests the minimum threshold for the onset of self-thinning generally occurs at relative densities around 60%. Our thinned stands were consistently below this boundary, while our unharvested stands averaged over 80% relative density during the final 21 years of the study. While relative density in controls increased steadily up to about 80% in 1982, high $MORT_{DEN}$ during measurement intervals with relative densities above this level contributed to a plateau in the size–density relationship during the last 21 years of the study. Mortality represented 15–98% of live biomass increment during this period, suggesting 80% relative density could be a threshold beyond which density-dependent mortality has biologically significant impacts on ecosystem processes related to productivity and carbon storage in red pine forests.

Mortality was generally lower in thinned stands than in unharvested controls, suggesting thinning effectively "captured" mortality by manipulating stand densities to keep SDI and relative density low while tree sizes increased over time (Drew and Flewelling, 1979). The effect of different thinning intensities (growing stock levels), however, was highly dependent upon the thinning method (from above, from below, or in combination) employed. This indicates any thinning effect on mortality was at least partly due to changes in stand structure and tree vigor associated with different thinning techniques. Thinning treatments generally reduced stand densities, and both the thin-from-below and combination thinning methods increased mean tree sizes compared to unmanaged stands. This was particularly evident in the thin-from-below treatments, where mortality was low throughout the study, regardless of growing stock level. A number of studies (Lorimer et al., 2001; Bigler et al., 2004, 2007; Busing, 2005; Fraver et al., 2008) suggest these demographic changes would favor greatly reduced mortality compared to stands composed of smaller, more densely spaced trees such as our control stands. Thinning to lower stocking levels did not seem to reduce mortality risk, and our results suggest excessive thinning in previously unthinned stands may initially increase mortality when paired with certain thinning methods. This could indicate a threshold response in stands thinned from above in which mortality reductions associated with decreased competition are offset by dramatic mortality increases resulting from exposure and mechanical damage during harvesting as growing stock levels are reduced from low (14 m^2 ha^{-1}) to very low (7 m^2 ha^{-1}).

High mortality rates in the 7 m^2 ha^{-1} thin-from-above treatment (the most intense removal) during the first 10 years following harvesting could be due to mechanical damage associated with preferentially harvesting and inadvertently felling large trees onto neighboring residual trees (Nyland, 1994; Caspersen, 2006). The drop in QMD following initial thinning in the 7 m^2 ha^{-1} thin-from-above treatment suggests the harvesting of large numbers of codominant and dominant trees in this treatment effectively shifted the population towards smaller trees with a greater risk of mortality from windfall and environmental stress (Bladon et al., 2007; Jönsson et al., 2007; Fortin et al., 2008; Thorpe et al., 2008). This could lead to high rates of mortality in the years following heavy initial thinning (Kariuki, 2008). Thinning from above may also have left a high number of low vigor residual trees that previously occupied intermediate to suppressed canopy positions, which could explain the increased mortality. A separate study at the same sites, however, found that productivity was typically higher in red pine stands that were thinned from above, especially at high thinning intensities (Bradford and Palik, 2009), and these red pine plantations had low percentages of intermediate and suppressed trees (Buckman et al., 2006) suggesting low tree vigor alone is an unlikely explanation for the initially high mortality found in the 7 m^2 ha^{-1} thin-from-above treatment. Whatever the cause, it is clear that excessive thinning may initially increase, rather than decrease mortality risk if the thinning method preferentially removes larger trees in codominant and dominant canopy positions. The absence of significant differences in mortality between stands that were thinned from above or thinned from below to moderate basal areas of 21–34 m^2 ha^{-1} suggests any detrimental effects associated with thinning methods were largely constrained to stands that received intense thinning treatments, and the effects were most pronounced in the ten years following the initial entry. The intermediate range of basal areas with low mortality also overlaps common guidelines for red pine management in the Lake States (Gilmore and Palik, 2005).

Our results also demonstrate the need for broader consideration of stand developmental processes as potential explanations for increased rates of background tree mortality in recent decades (e.g., van Mantgem et al., 2009; Allen et al., 2010). While some studies have shown that physiological responses to increased temperatures can explain certain die-off events (Adams et al., 2009; Breshears et al., 2009), or demonstrated clear linkages between climate and forest pest outbreaks that lead to elevated mortality (Williams and Liebhold, 2002; Greenwood and Weisberg, 2008; Kurz et al., 2008), many studies that have linked increased mortality rates to warming or drought through correlative evidence have not presented sufficient data regarding stand structural conditions to rule out developmental processes as potential drivers of mortality. We found significant positive correlations between tree mortality and temperature variables for our control stands coupled with rising temperatures during the study period, which could suggest the increase in temperatures contributed to rising mortality in our control stands during the later decades of the study. Our analysis of stand structural conditions, however, indicates the mortality trends we observed are readily explained by size–density relationships and self-thinning behavior rather than changes in temperature. While rising temperatures and water deficits undoubtedly contribute to increases in tree mortality rates worldwide (Allen et al., 2010), stand conditions and developmental processes should also be considered as potential drivers of mortality either alone, or through linkages with climate. Although our results document behavior in only one system and region, they represent the potential for erroneous conclusions if tree mortality studies evaluate correlations between mortality rates and climate variables without accounting for competitive interactions and stand developmental processes. Only through maintenance and access to long-term silvicultural studies, such as the one we examined, can these relationships be adequately quantified.

5. Conclusions

Our findings suggest thinning effectively reduced mortality in red pine, but the effects of different thinning methods must be weighed against desired growing stock levels if limiting mortality is a management objective. Thinning too intensely may result in an initial increase in mortality if the thinning method selectively removes larger, fast-growing trees and shifts populations towards smaller trees with increased mortality risk. Thinning from below may represent a better option for improving resilience, since this technique promotes residual stands composed of large, widely-spaced, fast-growing trees. Intermediate to high residual basal areas of 21–34 m^2 ha^{-1} appear to offer greater flexibility in response to different thinning methods, while still reducing mortality compared to unmanaged stands. Even in unharvested control stands, mortality had limited effects on productivity until relative densities exceeded 80%. Although increasing mortality rates in our unharvested controls were correlated with rising temperatures during the study period, principles of self-thinning based on tree size–density relationships appear to explain the mortality trends rather than any direct link to climate.

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Appendix A.

Mean stand and tree characteristics from a long-term red pine thinning study in Northern Minnesota, USA (see Tables A1–A3).

Table A1
Mean stand structural conditions by growing stock level treatment prior to initial harvesting in a long-term red pine thinning study in Northern Minnesota, USA.

	$7\ m^2\ ha^{-1}$	$14\ m^2\ ha^{-1}$	$21\ m^2\ ha^{-1}$	$28\ m^2\ ha^{-1}$	$34\ m^2\ ha^{-1}$	Control
Basal area ($m^2\ ha^{-1}$)						
Mean	40.80	42.09	40.66	40.02	40.25	41.50
Std. dev.	3.22	3.87	2.01	3.32	3.30	3.05
Min value	37.23	34.44	37.48	35.57	34.60	37.80
Max value	47.43	47.28	43.19	45.02	44.41	45.90
Stem density (stems ha^{-1})						
Mean	1271.17	1214.89	1289.02	1184.69	1286.28	1214.89
Std. dev.	167.64	91.83	424.34	104.55	155.11	178.08
Min value	1013.10	1062.52	988.39	1013.10	1124.29	1013.10
Max value	1519.64	1383.74	1593.77	1297.26	1544.35	1494.93
Quadratic mean diameter (cm)						
Mean	20.30	21.01	20.24	20.76	20.02	20.95
Std. dev.	1.21	1.11	1.60	0.78	1.20	1.11
Min value	18.78	19.43	18.57	19.43	18.59	19.20
Max value	21.65	22.28	22.97	21.71	21.59	22.30
Stand density index						
Mean	902.97	917.87	902.36	877.39	895.28	907.38
Std. dev.	71.07	72.45	64.83	69.09	70.22	73.60
Min value	803.02	774.97	834.92	788.55	789.00	816.31
Max value	1029.89	1013.76	989.38	978.35	994.17	1006.82
Relative density (%)						
Mean	62.57	63.61	62.53	60.80	62.04	62.88
Std. dev.	4.92	5.02	4.49	4.79	4.87	5.10
Min value	55.65	53.70	57.86	54.64	54.68	56.57
Max value	71.37	70.25	68.56	67.80	68.89	69.77
n	9	9	9	9	9	9

Table A2
Mean stand structural conditions and mortality rates by growing stock level treatment for a 46-year period of thinning in a long-term red pine thinning study in Northern Minnesota, USA.

	$7\ m^2\ ha^{-1}$	$14\ m^2\ ha^{-1}$	$21\ m^2\ ha^{-1}$	$28\ m^2\ ha^{-1}$	$34\ m^2\ ha^{-1}$	Control
Basal area ($m^2\ ha^{-1}$)						
Mean	15.23	26.59	25.43	32.29	39.35	55.16
Std. dev.	6.54	8.33	2.13	2.19	2.21	7.67
Min value	5.28	14.84	22.15	26.74	34.64	39.82
Max value	31.07	46.16	30.52	37.26	44.18	68.20
Stem density (stems ha^{-1})						
Mean	233.03	346.11	414.92	555.11	764.28	1079.50
Std. dev.	114.47	99.20	167.75	177.20	216.27	165.78
Min value	98.84	197.68	160.61	271.81	407.71	815.42
Max value	753.64	555.97	815.42	988.39	1321.91	1470.22
Quadratic mean diameter (cm)						
Mean	29.47	31.87	29.61	28.26	26.37	25.68
Std. dev.	5.58	6.65	5.93	4.60	3.88	2.84
Min value	16.65	19.19	19.54	20.32	19.40	20.09
Max value	42.78	47.73	44.15	38.39	35.45	31.82
Stand density index						
Mean	289.60	489.17	489.79	631.06	788.86	1110.45
Std. dev.	118.29	129.36	57.07	57.37	56.68	121.72
Min value	119.75	312.69	399.41	493.73	683.20	834.96
Max value	570.47	806.57	631.61	777.19	945.51	1311.09
Relative density (%)						
Mean	20.07	33.90	33.94	43.73	54.67	76.95
Std. dev.	8.20	8.96	3.96	4.00	3.93	8.43
Min value	8.30	21.67	27.68	34.21	47.34	57.86
Max value	39.53	55.89	43.77	53.86	65.52	90.85
Annual mortality (% stems)						
Mean	0.36	0.19	0.07	0.16	0.13	0.51
Std. dev.	1.21	0.41	0.18	0.56	0.27	0.72
Min value	0.00	0.00	0.00	0.00	0.00	0.00
Max value	8.46	1.71	0.78	3.33	1.50	5.94
Annual mortality (% biomass increment)						
Mean	6.50	2.67	1.44	8.10	2.51	21.74
Std. dev.	33.29	6.64	5.54	42.45	5.96	85.64
Min value	0.00	0.00	0.00	0.00	0.00	0.00
Max value	233.31	28.80	38.96	325.70	27.49	729.45
n	72	72	72	72	72	72

Table A3
Mean individual tree characteristics by growing stock level treatment for a 46-year period of thinning in a long-term red pine thinning study in Northern Minnesota, USA.

	7 m^2 ha^{-1}	14 m^2 ha^{-1}	21 m^2 ha^{-1}	28 m^2 ha^{-1}	34 m^2 ha^{-1}	Control
Diameter (cm)						
Mean	29.35	29.42	26.30	25.94	24.57	24.49
Std. dev.	8.38	7.25	6.39	5.32	4.94	5.06
Min value	9.14	9.40	8.64	9.65	9.91	9.40
Max value	50.29	49.78	45.72	41.91	40.39	40.13
Basal area increment (m^2 yr^{-1})						
Mean	0.0022	0.0019	0.0014	0.0012	0.0009	0.0006
Std. dev.	0.0013	0.0011	0.0009	0.0007	0.0005	0.0005
Min value	−0.0001	−0.0004	−0.0014	−0.0011	−0.0007	−0.0013
Max value	0.0116	0.0067	0.0063	0.0049	0.0034	0.0028
Relative basal area increment (%)						
Mean	3.3216	2.7985	2.6733	2.1559	1.7945	1.2320
Std. dev.	1.7113	1.3846	1.1560	0.9857	0.8611	0.7821
Min value	−0.6106	−1.2300	−2.9590	−1.9693	−1.4030	−3.1240
Max value	10.42	6.99	7.63	6.22	6.00	4.23
Relative DBH (%)						
Mean	40.52	39.06	38.82	38.92	39.06	38.78
Std. dev.	8.77	5.56	5.70	5.60	6.06	6.94
Min value	13.44	12.39	13.18	1.96	16.91	13.73
Max value	85.41	55.32	58.19	58.17	54.38	55.12

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